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FIFTY YEARS OF PROGRESS IN RESEARCH ON
SPECIES AND SPECIATION

By

Ernst Mayr

*Museum of Comparative Zoology, Harvard University,
Cambridge, Massachusetts 02138*

Marine Biological Laboratory/
Woods Hole Oceanographic Institution
Library

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Woods Hole, MA 02543

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Historians of science have taught us how much one can learn from studying the history of a field of science. This is excellently illustrated by the history of evolutionary biology as a whole, and by our growing understanding of species and speciation, in particular.

After 1859, two of Darwin's theories were accepted almost at once. First, evolution as such, and secondly, the branching theory of common descent. Natural selection was with almost equal unanimity rejected, being accepted only by a small group of naturalists. This was not too surprising since at that time no one understood variation and its origin. Finally, an active, almost violent, controversy developed over two other major Darwinian theories, that of speciation and that of evolutionary gradualism. As a matter of fact, Darwin himself was vacillating with respect to these two theories.

Let us now proceed to the year 1900 and the rediscovery of Mendel's laws. At that time, two camps became established in evolutionary biology. One consisted of the Mendelians represented by Bateson, DeVries, and Johannsen. They were strict typologists who saw discontinuity everywhere in nature and applied this correctly to

the nature of the genetic material, resulting in the theory of particulate inheritance. However, they drew from this the wrong conclusion as far as evolution is concerned, claiming that new species were produced by new mutations in a single saltation, completely rejecting Darwin's theory of gradualism. Their opponents were the biometricians, such as Pearson and Weldon, who correctly insisted on the gradualness of evolution but incorrectly claimed that inheritance was equally gradual, that is, blending. As far as genetics is concerned, the Mendelians were right; as far as evolution is concerned, the biometricians were right. There was no genuine population thinking in either camp and the biometricians and other opponents of Mendelism adopted Lamarckian inheritance in order to account for the gradualness of evolution.

In the ensuing years, the gap between the two camps narrowed appreciably as a result of the new findings of genetics and systematics. Eventually the biometricians disappeared from the scene and were replaced by a group of evolutionists I shall call the naturalists. At the same time the Mendelians were replaced by the population geneticists.

The major difference between these two new constellations of evolutionists was their sphere of interest. To document this it is necessary to define "evolution." The geneticists adopted a reductionist definition that, as we now see it, was quite misleading. They defined evolution as the change of gene frequencies in populations. This definition emphasized the wrong level of activity. Evolution is the story of adaptation, of the development of new kinds of animals and plants, of the origin of modes of reproduction, and of all aspects of the history of organisms. Evolutionary biology deals not merely with genes but with two major sets of problems: (1) the acquisition and maintenance of adaptedness, and (2) the origin and nature of organic diversity.

The geneticists dealt only with the problem of adaptedness. Their approach was reductionist, concerned with the genetic changes within a population. It dealt only with the time dimension, with what one might call "vertical evolution."

The naturalists concentrated on the other aspect of evolution, the nature of organic diversity. Their interest was in populations, species, and macroevolution, with particular emphasis on the process of speciation and the geographical components of evolution, what one might call the "horizontal dimension." This difference in basic concerns was, in my opinion, more important than their differences in the genetic interpretation.

There were also conspicuous national differences. Evolutionary genetics flourished in the Anglophone countries as indicated by the names T. H. Morgan, H. J. Muller, S. Wright, R. A. Fisher, and J. B. S. Haldane, while the study of organic diversity in an evolutionary manner flourished in Russia, Scandinavia, and Germany, but was poorly represented in English-speaking countries, in the United States by F. B. Sumner, L. R. Dice, D. S. Jordan, and J. Grinnell, and in England by E. Poulton and E. B. Ford.

We thus had two rather different traditions in the 1920s and early 1930s: an Anglophone genetic tradition studying the vertical component of evolution, that is, adaptive genetic change, and an essentially continental European tradition in systematics studying the horizontal component, that is the geographical changes of populations leading to speciation and macroevolution. As late as the early 1930s (up to 1935 and 1936), several authors declared that the gap between the two camps was unbridgeable. The confusion about

the causes of evolutionary change and speciation is well-documented by the widely read work of Robson and Richards (1936).

At that time there appeared on the scene a young beetle systematist who had grown up in the thinking of the Russian tradition with its emphasis on organic diversity but who also had had the advantage of nearly 10 years of work in (and stimulation by) an American laboratory in population genetics. I am, of course, referring to Theodosius Dobzhansky, who integrated the two great traditions I have just described and who produced what could almost be called the Bible of the evolutionary synthesis, his magnificent *Genetics and the Origin of Species* (1937). In spite of some omissions and even a few outright errors, this work contained the gist of the new paradigm of the evolutionary synthesis. Within a few years the synthesis was completed in zoology, as documented by the publications of J. Huxley (1942), E. Mayr (1942), G. G. Simpson (1944), and B. Rensch (1947). In 1950 G. Ledyard Stebbins brought in botany, showing in his monumental *Variation and Evolution in Plants* that the principles developed in the synthesis were equally applicable to plants, contrary to the claims of some other botanists. This is also true even for the numerous special phenomena and processes encountered in plants (Mayr and Provine 1980).

The synthesis of the 1930s–40s was the end of old arguments, in particular the final refutation of the various non-Darwinian theories of evolution, but it was also the beginning of a new set of controversies. My limitation of time permits me only to deal with those concerning species and speciation. Even under that limitation one has to cover scores of books and thousands of smaller publications. This forces me to present my findings as the final conclusions of long drawn-out arguments and perhaps seemingly in a rather dogmatic manner.

I am often asked, what in particular had been my own contributions to the Evolutionary Synthesis? They can be recorded under the two headings: species and speciation.

SPECIES

As far as species are concerned, I demonstrated the weakness, if not invalidity, of the previously most popular species criteria, particularly as stated in the morphological and genetical species

definitions. Instead, I promoted acceptance of the biological species concept with its emphasis on populations and on reproductive isolation: "A species is a group of interbreeding natural populations that is reproductively isolated from other such groups." I was not the first to adopt the biological species concept but there is little doubt that it was the support I gave it in my 1942 book that led to its rapid subsequent adoption. In particular, I pointed out the weakness of the morphological definition because it provided no criterion by which to determine the status of highly distinct intraspecific variants. Another weakness of the morphological definition was its inability to cope with a phenomenon for which I introduced the term "sibling species," that is, morphologically virtually identical populations that were nevertheless reproductively isolated. I expanded my treatment of sibling species in 1948 and 1963, and their extreme frequency is now generally acknowledged. Previously most of them, if recognized at all, had been listed as biological races. After 25 years of argument, I finally persuaded even Tracy Sonneborn to recognize the so-called varieties of *Paramecium* as sibling species. I believe there are some 14 such sibling species in the *Paramecium aurelia* group alone (Sonneborn 1975). Recent molecular studies have shown that most sibling species are as different from each other on a genetic-molecular basis as are morphologically distinct species.

The adoption of the biological species concept was perhaps even more important for the field worker. Ecologists and students of behavior usually work in a local situation, and there the recognition of species as non-interbreeding, coexisting populations is of the utmost importance. I also showed that in most species that are not host-specific, there is considerable geographic variation requiring the adoption of polytypic species. Such geographic variation may be clinal when populations are continuous, or discontinuous when populations, particularly peripheral populations, are spatially isolated from each other. Throughout I continued to emphasize that species are not types but populations.

The biological species concept, based as it is on population thinking, was not palatable to workers in several fields. The paleontologists, for instance, who study species in the time dimension, looked for a species concept that would be particularly suitable for the delimitation of fossil species. Here, Simpson (1961:153) proposed this

definition: "an evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary role and tendencies." The replacement of the clear-cut criterion of the biological species (reproductive isolation) by such undefined vague terms as "evolutionary tendencies" and "evolving separately" does not permit discrimination between good species and isolates. It is not applicable to polytypic species that contain geographical isolates. Nor does it even permit the delimitation of an "evolutionary species" within a phyletic lineage. (For a more detailed discussion see Mayr 1988a:323.) Simpson was not raised as a naturalist and, in spite of his biometric work on samples of fossils, his material did not allow a study of geographic speciation.

Another group of opponents of the biological species concept consisted of certain museum and herbarium taxonomists. They had to assign specimens to species, particularly such from widely distant geographic locations, and were puzzled what criteria to use in order to infer whether or not these isolates were reproductively isolated. As a result, they returned to a typological/morphological species concept. But this at once burdened them again with the two formidable deficiencies of the morphological species concept, the treatment of sibling species and of polymorphism. Both problems require a biological species concept for their resolution. Whatever decision one makes, it can only be inferred but not proven. The procedure of such inference is described in Mayr and Ashlock 1991:100–105.

Here I must make a short aside. Those who study species most intensely are naturalists working at a given locality. They study the interaction of species either as members of an ecosystem or in connection with the study of behavioral interactions among different species. The ranking of geographically distant populations is usually irrelevant for their objectives. For instance, for someone who studies the song sparrows of the San Francisco Bay region from the point of view of ecology, adaptation, or behavior, it is quite irrelevant whether one calls the song sparrows of the Aleutian Islands conspecific or a full species. However one ranks the Aleutian song sparrow will have no effect whatsoever on the study of the song sparrows of the San Francisco Bay region.

In a study of the over 600 species of North

American birds undertaken jointly with L. L. Short (1970), we found that with one single exception (*Pipilo*) all of them were fully consistent with the biological species concept. In a recent analysis of the vascular plants of Concord township in Massachusetts (Mayr 1992a), I found that the number of cases where the biological species concept led to an ambiguous decision was less than 10%. Even here, the difficulties were mostly those of insufficient scientific analysis rather than a consequence of using the biological species concept. Professor Stebbins has recently informed me that he found the number of species causing difficulties in two local floras to be around 4–6%. I am quoting these figures merely in order to make the point that the claim the biological species concept is inapplicable to plants is not substantiated when an actual analysis of a local flora is undertaken.

In their endeavor to apply cladistic principles even to intraspecific populations, that is to the very lowest branching points, some cladists have recently proposed a so-called “phylogenetic species” concept. Indeed there are now at least three versions of this concept in existence (Nixon and Wheeler 1990). This concept was first suggested by Rosen (1979:277) who proposed to consider the lowest population or population aggregate showing a new character (apomorphy) as a separate species: “a ‘species’ is merely a population or group of populations defined by one or more apomorphous features, it is also the smallest natural aggregation of individuals with a specifiable geographic integrity that can be defined by any current set of analytical techniques.” His definition would have required raising the population of just about every tributary of every Central American river to species rank, for nearly all of them have some special color gene or other peculiar characteristic. The most widely accepted definition of the phylogenetic species is: the smallest cluster of organisms which is diagnosably distinct from other such clusters. The real purpose of the phylogenetic species is to serve as “the smallest unit suitable for cladistic analysis” (Nixon and Wheeler 1990:212). I am not aware of any biological significance of this unit. To adopt this reductionist approach would lead to a massive increase in the number of recognized species in all groups with geographical variation and isolation. I estimate that birds would have over 20,000 phylogenetic “species,” as defined above, instead of the about 9,500 or so now recognized.

In other groups with many localized diagnosable populations the inflation might be even greater.

New papers supporting or proposing unorthodox species concepts continue to be published quite frequently, sometimes entire volumes stress such definitions (e.g., Otte and Endler 1989). As far as I am concerned, none of these proposals strikes me as particularly convincing. Coyne (1988), in a review in *Nature* of one of these volumes, refers to the commotion produced by the new proposals and then continues, “When the dust has settled only Mayr is still on his feet with his original concept remaining the simplest and most useful view of species.” For a while H. Paterson’s (1981) “recognition concept” was quite popular but neither Paterson himself nor anyone else seems to support it any longer after it was shown that, first, it did not really differ from the biological species concept, and secondly, that Paterson’s attack of the latter concept was based on a number of misconceptions (Mayr 1988b, and Coyne et al. 1988).

The major reason why it is impossible at this time to say the last word on species concepts is that the biological species concept is based on the study of diploid, sexually reproducing organisms, forming standard biological populations. Yet our knowledge of the population structure and mode of reproduction of many groups of lower invertebrates, lower plants, protists, and particularly prokaryotes is altogether insufficient. Many of them clearly do not fit the standard biological species concept. The place where the biological species concept runs into particular difficulties is in its application to asexually (uniparentally) reproducing organisms. These do not form populations in the sense of the populations of diploid sexually reproducing organisms, and therefore a species definition based on populations is inapplicable. It will be up to the specialists of such organisms to develop a species definition that is particularly suitable for them.

The question is often asked what influence molecular biology has had on our understanding of species and speciation. I conclude that it has made three major contributions.

First, it led to the discovery or confirmation of many sibling species. Biological races and other suspected sibling species were often shown by molecular methods to be just as different as morphologically highly distinct species. Furthermore, in the case of morphologically highly stable groups of species, relationships can sometimes

be worked out very reliably by molecular methods, and more than that, the branching point between various lineages can often be assigned to definite points in the geological time scale.

Second, when there is doubt concerning a particular variety, whether it is merely an intraspecific variant or a good species, molecular methods can usually give a clear-cut answer. No matter how different they may appear, intraspecific variants usually differ from other members of their population by only very few genes.

Third, in asexually reproducing organisms, molecular methods have cast a great deal of light on the amount of difference among various clones and on various cryptic methods of gene exchange.

It must be stressed that, opposing claims notwithstanding, molecular methods have not, in any way, weakened the biological species concept nor have they affected the standard interpretation of speciation.

SPECIATION

The recognition that species are populations, not types, was particularly important in the explanation of speciation. I reported in 1942 that in birds, mammals, butterflies, and snails, that is, in all taxonomically well-studied groups, speciation invariably turned out to have been geographical. This means that a population that had been isolated by geographical or vegetational barriers had acquired genetical isolating mechanisms during this geographical isolation and that this subsequently permitted it to coexist with the parental species without interbreeding. Here my studies of island faunas were particularly important because it enabled me to show that geographic speciation is a continuous process: populations on the most recently colonized islands are still almost identical with the source population while the longer an island population had been isolated, the more different it was, until finally after a sufficient time interval, complete species status had been reached.

How the isolating mechanisms were acquired continued to be controversial. There were two opposing theories, that of Alfred Russel Wallace, who thought they were acquired by selection when the previously isolated populations came into secondary contact, and that of Darwin, who said that selection could never complete the process of speciation under those circumstances. Dob-

zhansky favored the Wallace theory, Muller and I the Darwin theory. All the recent studies of secondary hybrid zones indicate that Darwin was, on the whole, right. Recent developments indicate that behavioral isolating mechanisms in animals may well be due to a change of function of properties acquired as a result of sexual selection during the previous isolation (Mayr 1988b).

In 1942 I distinguished four types of speciation: (1) geographical (allopatric), (2) semi-geographical (now called parapatric), (3) sympatric, and (4) instantaneous. I did not reject other forms of speciation outright, but I insisted that, as far as higher organisms are concerned, allopatric speciation was the most common mode. I think it is legitimate to state that this evaluation is still valid today. It is of interest to note that by far the longest chapter of my 1942 book was devoted to what I called the "biology of speciation," that is, all the ecological and behavioral factors involved. So far as I know there was no such treatment in the earlier literature.

Perhaps my major contribution was that I solved the old conundrum of how one could reconcile the sharp demarcation of species in a local fauna and flora with the Darwinian concept of gradual evolution. I demonstrated that in the local situation species are indeed sharply separated by gaps, but that if one looks at a species taxon in its total geographical representation through its entire range, one finds that most species consist of a large aggregation of local populations. Some of these, particularly those isolated at the periphery of the species range, are actually incipient species, that is, in transition from the status of local population to that of an independent new species. This refuted the old claim of Darwin's opponents that the sharp delimitation of local species, emphasized by naturalists from Linnaeus on, was incompatible with Darwin's concept of gradual evolution. The puzzle is solved by expanding the non-dimensional species of the local naturalist to the geographically variable species in a multi-dimensional approach. Furthermore this showed that it was unnecessary, indeed incorrect, to postulate speciation by saltation because geographic speciation is a gradualistic process.

To explain how new species originate had clearly been the most important objective of my *Systematics and the Origin of Species*. As is well known, Darwin had supported geographic speciation up to the 1840s but had become uncertain

when encountering certain situations in plants and eventually allowed for massive sympatric speciation (Mayr 1992b). And that was still the majority opinion among biologists when I gave the Jesup lectures in 1941.

The number of confusions existing at that time was considerable. Many authors, for instance, made *no* distinction between phyletic change (as observed by paleontologists) and an actual multiplication of species. Other authors, such as Goldschmidt (1940), in the tradition of the original Mendelians, still thought of speciation as a phenomenon involving a single individual giving rise to a new species.

Soon after 1942 it became clear to me that geographic speciation was not the simple unitary phenomenon I had first thought. I discovered that there are indeed two kinds of geographic speciation. In the classical type, now also called the dumbbell model or *dichopatric speciation*, the range of a more or less widespread species is divided by a barrier, resulting in two isolated parts of the species. These in due time may become sufficiently different to act toward each other as good species. The other mode, later called by me *peripatric speciation* (Mayr 1982), takes place when some dispersing individuals of a species establish an isolated founder population beyond the species periphery and this population becomes in due time sufficiently different and acquires the necessary isolating mechanisms to rank as a separate species.

Such speciation through the founder effect is of double significance. First, the genetic variation among the few founder individuals, sometimes only a single fertilized female, is only a small sample of the total genetic variability of the parental species. Inbreeding during the founder period will lead to further loss of genetic variability. This bottleneck effect may lead to a shift in epistatic interactions and to a considerable restructuring of the genotype. Such a genetic reorganization takes place only in maybe 1 out of 50 or 1 out of 500 of the founder populations. But if it takes place it provides an opportunity for major shifts in adaptation, particularly since the selecting factors in the founder population are apt to be quite different from those in the parental population. I arrived at this model of peripatric speciation *not* on the basis of theoretical considerations but rather because I observed that in South Sea islands' birds, nearly always the most isolated populations, or the populations most

distant from the core area of the species, tended to be the ones most different. Indeed, some of them were so different that they had been described as different genera (Mayr 1954).

And this indicates the second reason for the importance of peripatric speciation. It provides a bridge from speciation to macroevolution. I published these ideas in 1954, and Eldredge and Gould based their theory of punctuated equilibria on it in 1972. This theory, in its most simplified version, states that many seeming gaps in the fossil record are due to the fact that such highly localized events, as genetic reorganizations in founder populations, are not likely ever to be found in the fossil record, and secondly that after such speciation is completed and a new well-balanced genotype has been formed, evolution will greatly slow down and there may follow a period of stasis lasting millions of years. In the long controversy about punctuated equilibria, it would seem to me that more facts were published supporting the theory (in the simplified version here presented by me) than facts opposing it. However, most likely we have pluralism here as in most evolutionary phenomena, and in a few cases a phyletic lineage may drastically change in the course of time, also undergoing changes of macroevolutionary significance.

When we go back to the classical writings of Fisher and Haldane of the early 1930s we find that they, by only considering additive gene effects, assumed that evolution would proceed most rapidly in large, populous species. The more recent evidence refutes this belief. Let me add that the isolation of an incipient species has to be pretty nearly complete. Situations such as those described by Sewall Wright of temporarily isolated demes may contribute to the variability of a species, but not to the formation of new species.

Evolutionary changes corresponding to peripatric speciation take place also in refugia. As was first pointed out by Stresemann (1919), later by myself (1942), and more recently particularly by Haffer (1969), contracting relict populations resulting from climatic changes may also become incipient species and with a greatly accelerated rate of divergence during their period of reduced population size.

UNORTHODOX MODES OF SPECIATION

Even though geographic speciation was accepted by most evolutionists as by far the most

frequent mode of speciation, a minority of authors promoted the occurrence of alternate modes. One can assign these various proposals to three classes.

Instantaneous speciation occurs by the production of an individual that is reproductively isolated from the parental species. Actually, one type of instantaneous speciation, allopolyploidy, produced by the doubling of the chromosomes of a sterile species hybrid, is quite common in plants and not controversial. A different type of such instantaneous speciation is not infrequent in certain groups of animals, that is, a shift of species hybrids to parthenogenetic reproduction. Such cases have been particularly well analyzed in lizards and fishes (White 1974).

White (1978) proposed one further type of instantaneous chromosomal speciation, called by him *stasipatric speciation*. In this model, a new chromosome is produced through a chromosomal mutation which, although somewhat inferior as heterozygote, can conquer a new superior niche when homozygous. And then it can live side by side with the parental species owing to selection against the deleterious heterozygotes. White was led to this model by the observation that allopatric species in morabine grasshoppers invariably differ from each other in some chromosomal rearrangement that is inferior in the heterozygotes. However, as Key (1981), Mayr (1982), and others have since shown, White's model is not supported by any facts. If it were valid, one should find many cases of reproductively isolated new chromosome types inside the range of the parental species but one never finds this. It is far simpler to postulate, and this is supported by all known facts, that the chromosomal rearrangement takes place in a small founder population. The mistake made by White was to ask, is speciation chromosomal or geographical? In fact, however, all chromosomal speciation is simultaneously also geographical, and there is no difficulty in developing a model which combines both geographical and chromosomal speciation.

A second model not involving complete geographic isolation is so-called *parapatric speciation*. Here it is postulated that isolating mechanisms between two continuously distributed populations arise along an ecological escarpment. This model of speciation, particularly favored by Murray and Clarke (1980) and by Endler (1977), has not been substantiated in any of the very numerous test cases analyzed in recent

years. It is clearly associated with the Wallace-Dobzhansky theory of the sympatric origin of isolating mechanisms. The genetic analysis of numerous cases of secondary hybrid belts has shown that such belts are indeed secondary and do not lead to a gradual strengthening of the isolating mechanisms. The only seeming exceptions are cases of rapidly spreading species overrunning part of the range of a closely related species, a situation in which the first colonists have a greatly reduced opportunity for mating with conspecific individuals, with the result that occasional hybridization occurs. Such hybridization ends when the colonization is completed.

As far as the reinforcement of isolating mechanisms is concerned, one must make a distinction between species and populations. Where two closely related species overlap, indeed one finds sometimes a character divergence in the isolating mechanisms. On the other hand, it is now well established that gene flow and recombination prevent such an occurrence in the area of meeting of conspecific populations.

Finally, there is the possibility of *sympatric speciation*, that is, the development of isolating mechanisms within the cruising range of individuals of the parental species. As is well known, Darwin, for various reasons, finally accepted the widespread occurrence of sympatric speciation (Mayr 1992b). For 80 years it was considered the prevailing mode of speciation by most of his followers, particularly the entomologists. Even though some perceptive evolutionists, like Edward Poulton and particularly Karl Jordan, had refuted numerous putative cases of such sympatric speciation, it was still a popular, if not majority, belief in 1942. William Thorpe (1930), for instance, published several papers describing biological races believed by him to be incipient sympatric species. My own researches led me to claim in 1942, 1947, and 1963 that all these cases could be as well or better explained by geographic speciation and furthermore, that most so-called biological races were nothing but good biological species even though morphologically very similar, that is, they were sibling species. I never denied the possibility of sympatric speciation, but I denied that this form of speciation was indeed substantiated by the proposed cases. In recent years, Guy Bush has advanced a great deal of evidence believed by him to support sympatric speciation (Bush and Zwölfer 1984). He states, for instance, that there are more than 100,000

species of insects where mating and egg laying takes place on the host plant. He believes a shift to a new host plant might quickly result in sympatric speciation. He minimizes, however, the numerous difficulties as, for instance, the occurrence of back colonization of the parental host and the development of a two-host species, pointed out by various authors. Such difficulties disappear when one assumes that the host shift takes place in a founder population. Bush's evidence has been severely criticized by Futuyma and Mayer (1980), by Jaenike (1981), and by Paterson (1981). In the best studied case, the original host of the fruit fly species *Rhagoletis pomonella* is hawthorne (*Crataegus*). After the fly had colonized apple orchards around 1850, the apple population developed certain differences in life cycle and morphology from the original hawthorne population. However, vast monocultures, like apple orchards, provide an unusual situation. I spend my summers in southern New Hampshire, where there are square miles of apple orchards, and yet in all my botanizing in that area I have not yet found a single wild *Crataegus* tree. This population of *Rhagoletis* is therefore virtually isolated on apple trees.

Attempts were also made in the laboratory to produce sympatrically reproductively isolated species. One or two of these experiments, particularly one by Thoday, have indeed been seemingly successful (Thoday and Gibson 1962). However, there are literally scores of other such endeavors that led to negative results.

Disruptive selection has been suggested as an effective mechanism to produce different species. If we had within a single population different morphs specializing in different food sources, this might in due time lead to their isolation as different species, it was believed. Such cases of trophic polymorphism have indeed been found in various species of fishes, particularly cichlids (Meyer 1990) and in a species of birds (Smith 1990). However, in none of the cases is there any indication of a development of isolating mechanisms between the trophic types. Indeed, as a Darwinian, one should expect that a lineage having both trophic types would have greater inclusive fitness than one giving up one of the two sources of food. This would be true in any variable environment, and that of course means it is true for all environments.

Up to now the best evidence for sympatric speciation is provided by ants, where sometimes

in a flourishing colony of one species, inquilines of another species are found (Buschinger 1990). The latter are so-to-speak parasitic because they have no worker caste and benefit from the labor of the workers of the host species. In the few cases that have been well described, the inquiline species seems to be most closely related to the host species and there is no mode of geographic speciation that could produce such a result.

In spite of all these advances and clarifications, there are still areas of great uncertainty. For instance, how do pelagic species speciate? Each of such species is usually associated with a particular water mass, but how can such a species be divided into two? There is a possible scenario. One can assume that some peripheral portion of such a water mass becomes isolated by a different water mass intervening between it and the remainder of the species population and that eventually this isolated population acquires species status. However, except for one or two cases of fossil species, there is so far very little evidence indicating the validity of this scenario.

As in the case of species, our conclusions about speciation are based on the situation in diploid sexual species. There is still great uncertainty about speciation in asexual organisms, particularly in view of the fact that it is so uncertain what a species is in these organisms. Hence, what is speciation? However, we have the fact of the bdelloid rotifers, a taxon with some 200-odd species, all of them asexual with no males ever encountered. This is best explained by the assumption that there is a continuing production of asexual clones, and that subsequent extinction of the less-viable clones leads to gaps between what ultimately will be called species.

GENETICS OF SPECIATION

In view of the intensive work on speciation during the last 100 years, it is shocking to have to admit how little we actually know about the genetics of speciation. This has a number of reasons. The first is that many geneticists did not fully understand the difference between phyletic change and multiplication of species. They thought that by extrapolating from the changes within a gene pool they would be able to explain speciation. However, it is now quite clear that the solution will come from a comparison of different populations. Everything we know, particularly through the study of peripatric speciation,

indicates that certain genetic turnovers may go on in a founder population that are not encountered in a normal species population. The second reason for the slow progress is the heterogeneity of the genotype. Owing to the ease of the electrophoresis method, most authors have studied the variation of enzyme genes. However, there is no evidence that this class of genes is particularly involved in the origin of isolating mechanisms. On the contrary, many of the enzyme alleles are apparently in Kimura's class of quasi-neutral genes. It would certainly be misleading to base one's explanation of speciation on this class of genes. There is much to suggest that the genes for behavioral isolating mechanisms belong to different classes of genes from the genes for sterility factors. But very little concrete evidence on these classes of genes is available.

There is little hope for a valid explanation of the genetics of speciation until genes are classified into different categories, some of which do and some of which do not play a role in speciation. Furthermore, it is quite likely that different kinds of genes are involved in the speciation of different kinds of organisms. The work on the African cichlid fishes indicates that behavior genes may be very important in this taxon, becoming isolating mechanisms by way of sexual selection, and may permit the evolution of reproductively isolated populations within incredibly short periods, periods of only a couple of hundred years (Mayr 1988a). On the other hand, the conspecificity of certain eastern North American plants with their representatives in eastern Asia indicates that in this case an isolation of 5, 8, or 10 million years was not sufficient for the origin of efficient isolating mechanisms. Wherever we have drastically different rates of speciation, one can be reasonably sure that different kinds of isolating mechanisms and their genetics are involved.

SUMMARY

In conclusion, I think it is legitimate to say that the basic picture of species and speciation developed by taxonomists during the Evolutionary Synthesis and presented in 1942 in my book *Systematics and the Origin of Species* did not have to be changed subsequently. Most of the attacks against it have been thoroughly refuted, even though there have been clarifications and the development of a more pluralistic approach. However, there are still vast uncertainties, par-

ticularly with respect to the lower invertebrates, lower plants, fungi, prokaryotes, and also such ecological specialists as pelagic animals. Finally, the area where there is perhaps still the greatest uncertainty is the genetic basis of the isolating mechanisms. But here again the researches are not likely to lead to any refutation of currently accepted views. To repeat, the concepts of species and speciation as developed during the evolutionary synthesis are likely to endure.

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